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Muscle contributions to support and progression over a range of walking speeds

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ABSTRACT

Muscles actuate walking by providing vertical support and forward progression of the mass center. To quantify muscle contributions to vertical support and forward progression (i.e., vertical and fore-aft accelerations of the mass center) over a range of walking speeds, three-dimensional muscle-actuated simulations of gait were generated and analyzed for eight subjects walking overground at very slow, slow, free, and fast speeds. We found that gluteus maximus, gluteus medius, vasti, hamstrings, gastrocnemius, and soleus were the primary contributors to support and progression at all speeds. With the exception of gluteus medius, contributions from these muscles generally increased with walking speed. During very slow and slow walking speeds, vertical support in early stance was primarily provided by a straighter limb, such that skeletal alignment, rather than muscles, provided resistance to gravity. When walking speed increased from slow to free, contributions to support from vasti and soleus increased dramatically. Greater stance-phase knee flexion during free and fast walking speeds caused increased vasti force, which provided support but also slowed progression, while contralateral soleus simultaneously provided increased propulsion. This study provides reference data for muscle contributions to support and progression over a wide range of walking speeds and highlights the importance of walking speed when evaluating muscle function.

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1. Introduction

Many individuals with neuromuscular impairments walk slowly (Turnbull et al., 1995; Abel and Damiano, 1996; Goldie et al., 1996; Dingwell et al., 2000). Evaluating a patient's gait requires discriminating between deviations caused by pathology and walking speed. Several studies identified how walking speed influences joint kinematics (Murray et al., 1984; Kirtley et al., 1985; Holden et al., 1997; Stansfield et al., 2001b; van der Linden et al., 2002; Nymark et al., 2005; Schwartz et al., 2008), ground reaction forces (Andriacchi et al., 1977; Jansen and Jansen, 1978; Vaughan et al., 1987; Stansfield et al., 2001a; Schwartz et al., 2008), and muscle activity (Murray et al., 1984; Shiavi et al., 1987; Hof et al., 2002; den Otter et al., 2004; Nymark et al., 2005; Cappellini et al., 2006; Schwartz et al., 2008). However, the mechanisms by which muscles modulate the accelerations of the

mass center over a range of walking speeds are not well understood.

Several studies have examined how muscles provide support and progression (Pandy, 2001; Neptune et al., 2004; Liu et al., 2006) at a typical walking speed in unimpaired adults. Using a computer simulation of overground walking, Liu et al. (2006) found that gluteus maximus, vasti, and dorsiflexors slowed the body mass center during early stance; gluteus medius, soleus, and gastrocnemius propelled the mass center forward during late stance. The same muscles modulated vertical acceleration of the body mass center. Their findings agreed with those of other researchers (Pandy, 2001; Anderson and Pandy, 2003; Neptune et al., 2004). A drawback to all of these previous simulation studies, however, is that each analyzed only one simulation at one walking speed, making it difficult to generalize the results to the larger population who walk at various speeds.

Neptune et al. (2008) recently analyzed two-dimensional computer simulations of walking at five speeds and found that vertical support of the trunk was provided by gluteus maximus, vasti, soleus, and gastrocnemius, while forward propulsion of the trunk was provided by soleus and rectus femoris. Neptune et al. (2008) were able to precisely control subject walking speed using

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a treadmill; however, there are differences between overground and treadmill walking (Murray et al., 1985; Lee and Hidler, 2008).

We examined the mechanisms that modulate vertical (support) and fore-aft (progression) accelerations of the body mass center at different overground walking speeds. We quantified how the contributions of individual muscles to mass center accelerations vary with walking speed by creating and analyzing 32 three-dimensional, muscle-actuated simulations of walking, representing eight different subjects walking at four speeds.

2. Methods

To examine the contributions of muscles to the acceleration of the mass center, we acquired subjects' gait analysis data at four walking speeds. These data were used to generate subject-specific simulations at each walking speed (Fig. 1). We calculated muscle contributions to support and progression with a perturbation analysis (Liu et al., 2006). A repeated measures analysis of variance identified the effects of walking speed on muscle contributions to mass center accelerations.

We generated simulations of eight subjects, each walking at four speeds (Table 1). Protocols for measuring ground reaction forces, kinematics, and electromyographic (EMG) patterns are reported by Schwartz et al. (2008). The ground reaction forces were sampled at 1080 Hz and low-pass filtered at 20 Hz. The EMG data were sampled at 1080 Hz, band-pass filtered between 20 and 400 Hz, rectified, and then low-pass filtered at 10 Hz. The resulting envelope for each muscle was normalized by the peak value recorded from that muscle over all walking speeds for a given subject.

The walking speed for each trial was categorized post-hoc as very slow, slow, free, or fast:

$$\begin{aligned} \text{very slow} & 0 < v^* \leq \bar{v}_{\text{free}}^* - 3\sigma_{\text{free}}^* \\ \text{slow} & \bar{v}_{\text{free}}^* - 3\sigma_{\text{free}}^* < v^* \leq \bar{v}_{\text{free}}^* - \sigma_{\text{free}}^* \\ \text{free} & \bar{v}_{\text{free}}^* - \sigma_{\text{free}}^* < v^* \leq \bar{v}_{\text{free}}^* + \sigma_{\text{free}}^* \\ \text{fast} & \bar{v}_{\text{free}}^* + \sigma_{\text{free}}^* < v^*, \end{aligned}$$

where nondimensional walking velocity $v^* = v/\sqrt{gL_{\text{leg}}}$ (v is absolute walking velocity, L_{leg} is leg length, and g is gravitational acceleration; Hof, 1996), and \bar{v}_{free}^* and σ_{free}^* are the mean and standard deviation, respectively, of the nondimensional free walking speed of the subject cohort reported by Schwartz et al. (2008). The eight subjects from this cohort achieved at least one double-stance phase on the force plates at each walking speed, which provided the bilateral ground reaction force data necessary to analyze the double-stance phase with the simulation method used in this study.

We used the OpenSim software to simulate each walking trial (Delp et al., 2007). A generic musculoskeletal model with 23 degrees of freedom, actuated by 92 muscle-tendon compartments (Delp et al., 1990; Thelen and Anderson, 2006), was scaled to match the anthropometry of each subject. Subtalar and metatarsophalangeal joints were locked at neutral anatomical angles. External forces and moments (i.e., residuals) were applied to the pelvis segment to compensate for dynamic inconsistencies between the measured kinematics and the measured ground reaction forces (Kuo, 1998). We reduced the magnitudes of these residuals by slightly altering the model's mass and the kinematics to be tracked (Delp et al., 2007). Computed muscle control was used to compute the actuator excitations required to track the experimental lower limb kinematics (Thelen et al., 2003); constraints on the excitations were used when needed to ensure that the simulated excitations were consistent with the experimental EMG envelopes and EMG patterns from the literature (Perry, 1992; Hof et al., 2002; den Otter et al., 2004; Cappellini et al., 2006; Schwartz et al., 2008).

A perturbation analysis was used to compute the contributions of individual muscles to the vertical and fore-aft accelerations of the body mass center (Liu et al., 2006). Throughout each simulated walking trial, the nominal force of each muscle actuator was increased by 1 N, the simulation was integrated forward for 0.03 s, and the mass center position was computed. This perturbed position and the unperturbed mass center position were used to calculate an average change in linear acceleration due to the perturbation per unit muscle force, which was then scaled by the actuator's unperturbed force to produce an estimate of the mass center acceleration contributed by the actuator. To allow changes in the ground reaction forces and moments during the perturbation, we added spring-damper elements between the model's feet and the floor.

To simplify data analysis, we summed across smaller actuator compartments that performed similar functions. For example, contributions from the three compartments of gluteus maximus were summed into a single gluteus maximus contribution. Similarly, a dorsiflexor contribution comprised contributions from tibialis anterior, extensor digitorum longus/brevis, and extensor hallucis.

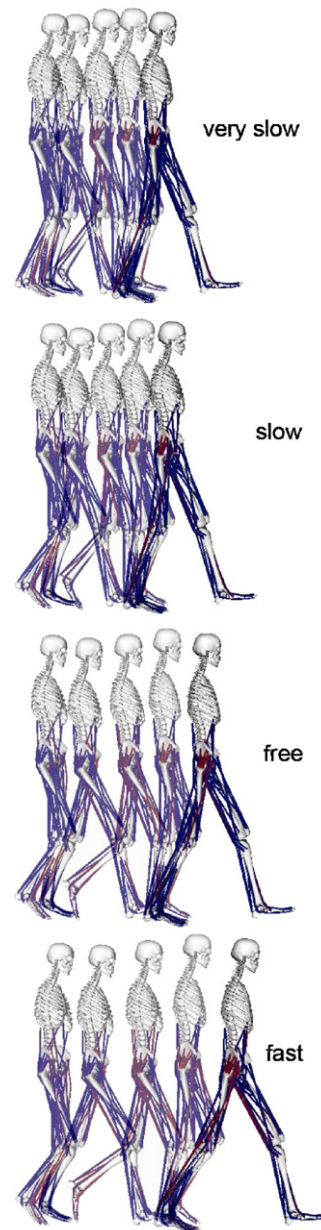


Fig. 1. Musculoskeletal model used to generate three-dimensional simulations of walking for eight subjects, each walking at four speeds (very slow, slow, free, and fast). Shown here are still images from simulations of a representative subject. Each simulation begins during left foot single-limb stance and ends at left terminal swing. The muscle actuator colors indicate the level of activation on a scale from dark blue (no activation) to bright red (full activation).

Each simulation began during single-limb stance, continued through double-limb stance, and ended in terminal swing of the same limb (Fig. 1). We time-shifted muscle contributions from the left and right sides to approximate continuous muscle function over a complete gait cycle, using a time-weighted averaging function to blend the data when they overlapped. The perturbation method did not allow a direct decomposition of the ground reaction forces beneath each foot. The ground reaction forces beneath the foot are due predominantly to muscle forces in the ipsilateral leg (as opposed to the contralateral leg; Anderson and Pandy, 2001). Thus, as an approximation, to attribute the appropriate portion of the ground reaction force to individual muscles during double-limb stance, we assumed that muscles in the right limb act via the right foot-floor interactions and muscles in the left limb act via the left foot-floor interactions. Contributions from trunk muscles were distributed to both feet in proportion to the fraction of the total ground reaction force applied under each foot throughout double-limb stance.

Table 1
Subject characteristics and walking speeds

Subject	Gender	Age (years)	Mass (kg)	Leg length (m)	Very slow speed (m/s) (nondimensional) ^a	Slow speed (m/s) (nondimensional) ^a	Free speed (m/s) (nondimensional) ^a	Fast speed (m/s) (nondimensional) ^a
1	F	10.2	41.1	0.77	0.57 (0.21)	0.67 (0.24)	1.01 (0.37)	1.40 (0.51)
2	F	14.6	66.0	0.90	0.49 (0.16)	0.80 (0.27)	1.21 (0.41)	1.52 (0.51)
3	M	13.8	41.6	0.84	0.55 (0.19)	0.70 (0.24)	1.29 (0.45)	2.00 (0.70)
4	F	11.3	32.4	0.72	0.49 (0.19)	0.94 (0.35)	1.15 (0.44)	1.34 (0.50)
5	F	14.1	81.9	0.81	0.50 (0.18)	0.81 (0.29)	1.11 (0.39)	1.42 (0.50)
6	F	14.5	61.9	0.94	0.56 (0.19)	0.70 (0.23)	1.12 (0.37)	1.62 (0.53)
7	F	18.0	63.1	0.84	0.61 (0.21)	0.80 (0.28)	1.17 (0.41)	1.64 (0.57)
8	M	7.0	26.1	0.66	0.56 (0.22)	0.61 (0.24)	1.15 (0.45)	1.51 (0.60)
Mean		12.9	51.8	0.81	0.54 (0.19)	0.75 (0.27)	1.15 (0.41)	1.56 (0.55)
Standard deviation		3.3	19.2	0.09	0.04 (0.02)	0.10 (0.04)	0.08 (0.03)	0.21 (0.07)

^a Speeds are reported in m/s and nondimensional units (actual speed normalized by $\sqrt{gL_{leg}}$).

We estimated the contributions to support and progression from skeletal alignment by subtracting the accelerations due to muscles from the accelerations due to ground reaction forces. This quantity represents the resistance provided by the skeleton to the acceleration of gravity. It also includes contributions from centrifugal accelerations, which were assumed to be relatively small (Anderson and Pandy, 2003).

We performed a one-way repeated measures analysis of variance (SPSS Inc., Chicago IL), using walking speed as the within-subjects variable, to test whether walking speed had a significant effect on the peak contributions to mass center accelerations for selected muscles. For cases in which the data violated sphericity assumptions, the Huynh-Feldt epsilon was applied as a correction (Ho, 2006). If the main effect of walking speed was significant, within-subject repeated contrasts were analyzed to test whether significant differences in peak muscle contributions to mass center accelerations existed between successive speed pairs (i.e., very slow to slow, slow to free, free to fast). The significance level for all tests was $\alpha \leq 0.05$.

3. Results

The simulated joint angles for pelvis, hips, knees, and ankles tracked the experimental data with a maximum error of 3° across all 32 simulated walking trials (Fig. 2). The simulated joint moments computed by summing the moments generated by muscle actuators at each joint closely matched the experimental joint moments computed by inverse dynamics (Fig. 3). The experimental EMG data for the subjects were highly variable. The simulated muscle activations captured some of the consistent speed-related trends (Fig. 4). For example, quadriceps activity in early stance and plantarflexor activity in late stance increased with walking speed in both the simulations and the EMG data.

The vertical and fore-aft mass center accelerations during walking at a free speed were generated primarily by muscles (Fig. 5; compare “GRF/kg” and “muscle” accelerations at free speed). During double-limb stance, muscles in both limbs provided vertical support, while the muscles in the leading limb resisted progression and the muscles in the trailing limb assisted progression. Muscles provided vertical support while resisting progression in early single-limb stance and assisting progression in late single-limb stance.

The magnitudes of the muscle contributions to mass center accelerations changed with walking speed (Fig. 5; “muscles” row). Decreasing walking speed from free to slow caused dramatic reductions in contributions to support, in resistance to progression from muscles in the leading limb, and in assistance for progression from muscles in the trailing limb. Instead, acceleration of the mass center was influenced more by the resistance to gravity provided by skeletal alignment. In particular, slow walking was characterized by a

more extended leading limb, as can be seen in the reduction of knee flexion angle during early stance from ~23° during free walking to ~10° during slow walking (Fig. 2; knee flexion at ~10% of gait cycle).

Walking speed significantly affected support contributions from gluteus maximus, gluteus medius, hamstrings, vasti, and soleus (Table 2). Walking speed significantly affected progression contributions from gluteus maximus, vasti, gastrocnemius, and soleus. With the exceptions of progression contributions from the gluteus maximus and gastrocnemius, all of these muscle contributions showed significant differences (support or progression) for comparisons between successive walking speeds.

The influence of walking speed was most apparent when comparing muscle contributions during slow and free walking speeds (Figs. 6 and 7). Support contributions from vasti increased dramatically when walking speed increased from slow to free (Fig. 6A). Support contributions also increased from gluteus maximus, hamstrings, and soleus. Gluteus medius, by contrast, exhibited a small decrease in support contributions when walking speed increased from slow to free (Fig. 6A). Contributions from vasti to resist progression and from soleus to assist progression increased significantly (Fig. 6B).

Only two muscles exhibited significant increases in contributions when walking speed increased from very slow to slow: gluteus maximus provided more support (Fig. 6A) and soleus provided greater assistance to progression (Fig. 6B). When walking speed increased from free to fast, support contributions increased significantly from gluteus maximus, vasti, and soleus (Fig. 6A). Vasti's resistance to progression in early stance also increased during fast walking (Fig. 6B).

Contributions from rectus femoris and dorsiflexors to mass center accelerations were not significantly affected by walking speed (Fig. 7). At all speeds, rectus femoris made modest contributions to support, while resisting progression through most of stance. Dorsiflexors made large contributions to support, while resisting progression in early stance.

4. Discussion

We identified the muscles primarily responsible for modulating vertical support and forward progression over a range of walking speeds in unimpaired children. In general, muscle contributions to support and progression increased with walking speed, with especially large increases in vasti contributions between slow and free walking. During very slow and slow

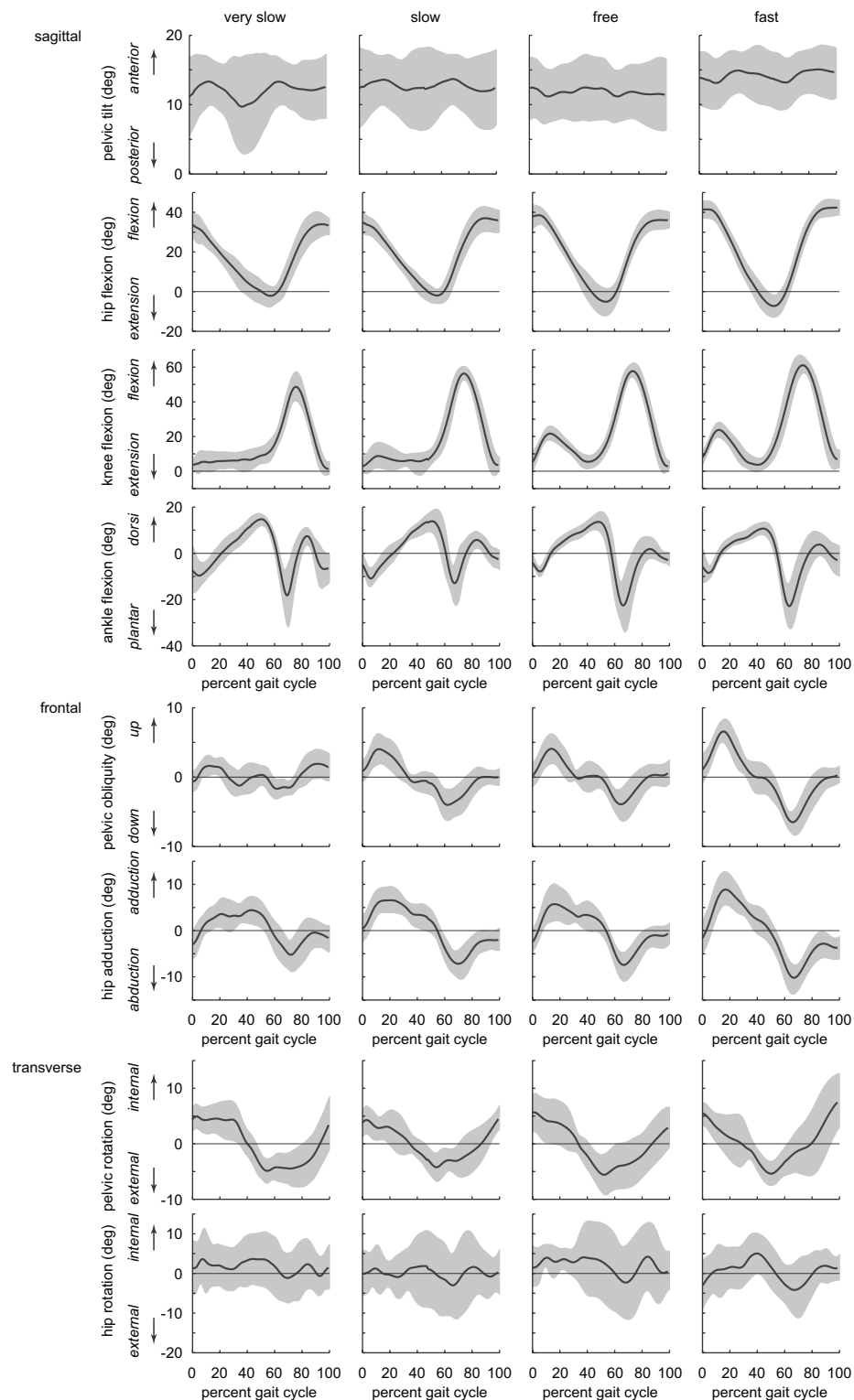


Fig. 2. Joint angles across walking speeds. The shaded area spans the mean \pm one standard deviation of the experimental joint angles for eight subjects. The black line represents the mean simulated joint angles for eight subject-specific simulations.

walking, a straighter limb in early stance—rather than muscle—provided a majority of the support against gravity.

These results illustrate similarities and differences between simple and complex dynamic walking models. For example, consistent with the observed redirection of the mass center

velocity in simple models (Donelan et al., 2002), we observed propulsive influences from trailing limb muscles and slowing influences from leading limb muscles during double-limb stance. Using a simple model with rigid limbs, Donelan et al. (2002) demonstrated that a force applied to the trailing limb efficiently

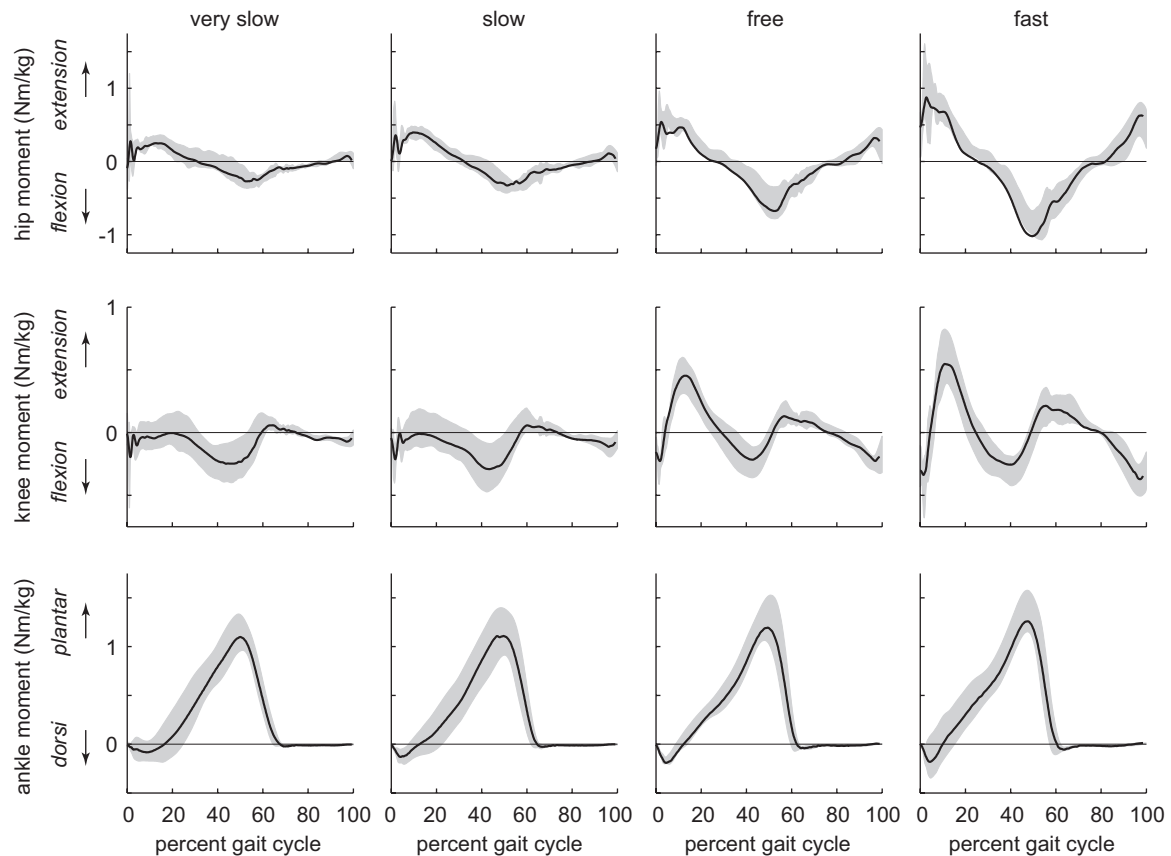


Fig. 3. Sagittal hip, knee, and ankle moments across walking speeds. The shaded area spans the mean \pm one standard deviation of the mean moments, normalized by body mass and computed with inverse dynamics from conventional gait analysis for eight subjects. The black line represents the mean simulated joint moments for eight subject-specific simulations, normalized by body mass and computed by summing the moments produced by individual muscle actuators.

redirects the mass center velocity; we found that gastrocnemius and soleus played this role. In simple models, the slowing influence of the strut-like leading limb arises from the passive transmission of the ground reaction force to the mass center (McGeer, 1990; Collins et al., 2001; Kuo, 2002). Indeed, at slower speeds, we observed that skeletal alignment served a function similar to a strut. At faster walking speeds, the differences between simple and complex models are apparent. As stride length and walking speed increase, the magnitude of the fore-aft ground reaction force during early and late stance increases, and causes larger slowing and propulsive forces, respectively. We found that gastrocnemius and soleus provided the required increased propulsion from the trailing limb. However, the human leading limb is no longer strut-like at faster walking speeds, due to knee flexion, and cannot passively transmit the ground reaction forces. The resulting limb compliance is represented in modified simple models with a compressive spring in line with the strut (Lee and Farley, 1998; Srinivasan and Ruina, 2006), but knee flexion in humans requires active modulation by vasti, which—along with gluteus maximus—provide the slowing force from the leading limb. Walking with flexed knees incurs an increased energetic cost (Winter, 1983), which may be offset by gains in limb stability (Seyfarth et al., 2001; Gunther et al., 2004), improved shock absorption, or other benefits. Future simulation studies may provide a useful framework for comparing the energetic costs of walking with flexed knees versus the potential benefits of making use of passive walking dynamics.

The influence of walking speed on ground reaction forces has been well-documented (Andriacchi et al., 1977; Jansen and Jansen, 1978; Vaughan et al., 1987; Stansfield et al., 2001a; Schwartz et al., 2008), and this study demonstrates how muscles and skeletal resistance to gravity give rise to reaction forces at different walking speeds. Previous studies variously identified gluteus maximus, gluteus medius, vasti, hamstrings, gastrocnemius, soleus, and dorsiflexors as important modulators of vertical and fore-aft (Neptune et al., 2004; Liu et al., 2006) ground reaction forces or mass center accelerations during walking at a typical speed. We observed similar results for the free walking speed in this study. The greater peaks of vertical and fore-aft ground reaction forces at faster walking speeds arise from greater forces in the vasti and gluteus maximus in early stance and greater forces in the soleus and gastrocnemius in late stance. The observation that the accelerations produced by these muscles increased with walking speed is consistent with the fact that the magnitude of muscle activity generally increases with speed (Murray et al., 1984; Shiavi et al., 1987; den Otter et al., 2004). Our results concur with those of Neptune et al. (2008), who observed that gluteus maximus, vasti, gastrocnemius, and soleus were important for trunk support over a range of walking speeds, and that soleus contributions to the trunk propulsion increased substantially with speed.

Gluteus medius support contributions were relatively constant across walking speeds. This agrees with van der Linden et al.'s (2002) observation that hip abduction moment neither increases

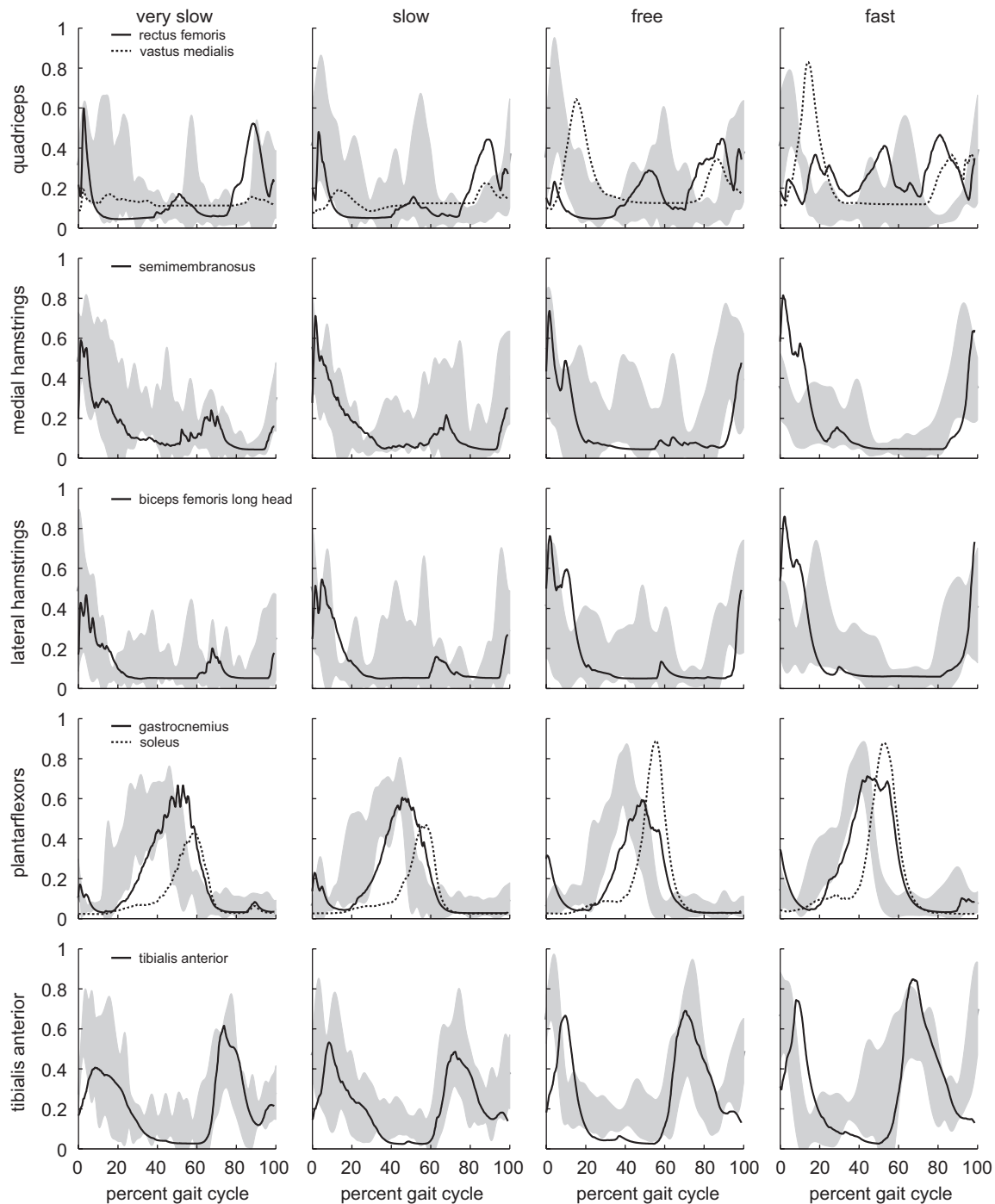


Fig. 4. Comparison of experimental and simulated muscle activity across walking speeds. The shaded areas represent the mean \pm one standard deviation of the EMG linear envelopes recorded for eight subjects. The solid and dotted lines represent the mean simulated muscle activations for eight subjects. Each row includes the EMG data for one surface electrode and simulated activations for representative muscle actuators.

nor decreases consistently with walking speed. In our simulations, gluteus medius provided support while the foot was flat on the floor; after heel-off it pulled the mass center downwards. It is unclear whether this downward acceleration, especially during swing, is an accurate reflection of gluteus medius function. Although gluteus medius is primarily active during stance, swing phase activity can occur (Shiavi et al., 1987), and our optimization algorithm often activated it during late stance and swing.

Similarly, the directions of dorsiflexor accelerations were sensitive to the timing of forefoot contact in early stance, which was variable across walking trials. Therefore, even though the magnitude of dorsiflexor muscle activity consistently increased with walking speed, its contributions to support and progression were variable.

Neptune et al. (2008) found that the hip flexors, iliopsoas and rectus femoris, made larger contributions to swing initiation and

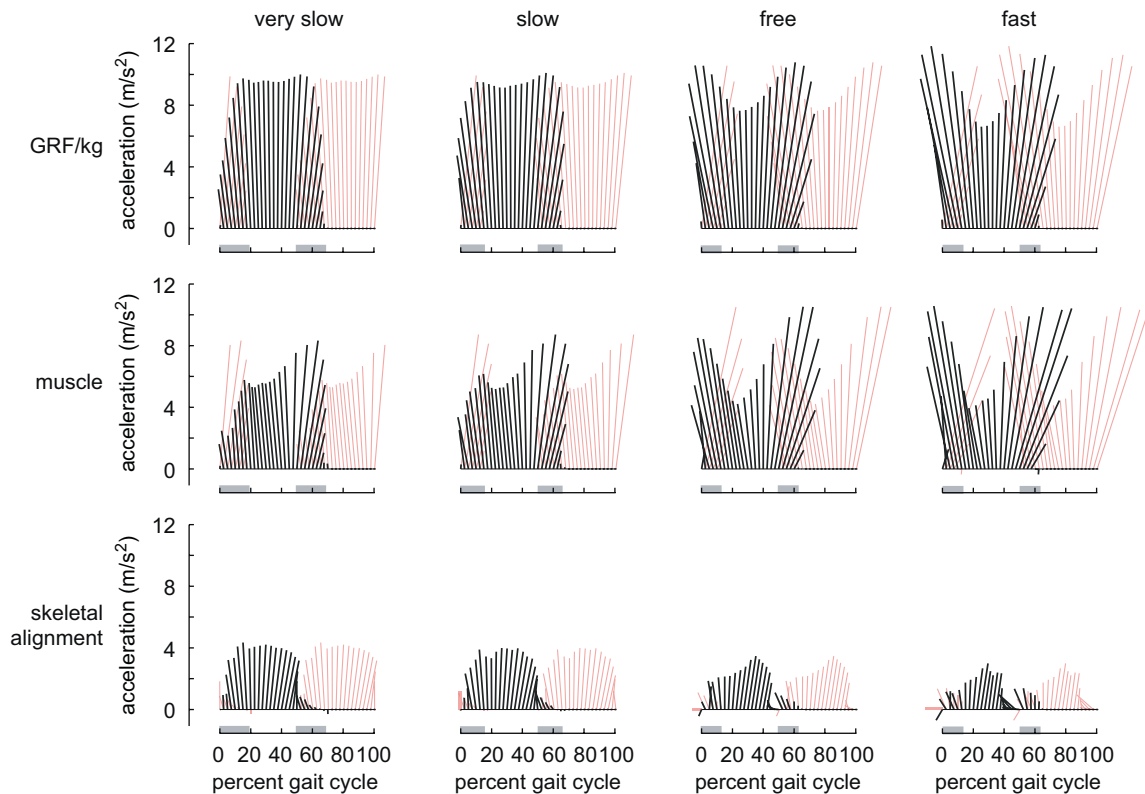


Fig. 5. Contributions to the acceleration of the body mass center from ground reaction forces, muscles, and the resistance to gravity by skeletal alignment across walking speeds. Each ray is the resultant vector of the vertical and fore-aft accelerations, averaged across eight subjects. The black vectors represent the accelerations attributable to the ground reaction force, muscles, or skeletal alignment from the limb undergoing initial contact at 0% of the gait cycle. The red vectors represent accelerations from the contralateral limb. The shaded bars indicate periods of double-limb stance.

Table 2

Muscles that exhibited significant speed effects on peak contributions to support and progression

Muscle	Support		Progression	
	F^a	p	F^a	p
Gluteus maximus	23.59	< .001	4.82 ^b	.042
Gluteus medius	3.29	.041	–	–
Hamstrings	8.13	.001	–	–
Vasti	39.74	< .001	49.59	< .001
Gastrocnemius	–	–	11.94	< .001
Soleus	34.79	< .001	69.71 ^c	< .001

^a Value of the F ratio for one-way repeated measures analysis of variance. Numerator and denominator degrees of freedom are 3 and 21, respectively, unless otherwise indicated.

^b Numerator and denominator degrees of freedom are 1.46 and 10.21, respectively, following the Huynh-Feldt correction.

^c Numerator and denominator degrees of freedom are 1.65 and 11.53, respectively, following the Huynh-Feldt correction.

trunk propulsion, respectively, as walking speed increased. Our analysis of body mass center accelerations suggested that these muscles may be more important for modulating the dynamics of individual body segments during walking, rather than for moving the entire body mass.

Our results should be interpreted in light of several limitations. Although we did not explicitly simulate arm motion, the residual

forces and moments applied to the model are intended, in part, to apply external forces that represent the effects of upper extremity dynamics. Arm motion affects the moments between the trunk and lower extremity, although the magnitude of this influence is diminished at slower walking speeds (Li et al., 2001). We attempted to minimize the errors in trunk dynamics by reducing residual forces and torques (Delp et al., 2007), rather than eliminating them completely (Thelen and Anderson, 2006). The latter technique, which resolved dynamic inconsistencies solely by changing kinematics, can cause large errors in the simulated trunk motion. By allowing some residuals, we simulated appropriate trunk motion while improving dynamic consistency. Additional work is needed to better understand how arm motion affects the analysis of walking simulations. Another limitation is that musculoskeletal model does not account for slow and fast twitch fiber distributions within muscles. For example, soleus has a larger fraction of slow twitch fibers than gastrocnemius (Edgerton et al., 1975), so a reasonable expectation is that soleus would provide most of the plantarflexor support and progression at slower walking speeds, with gastrocnemius assisting at faster walking speeds. Our results did not reflect this coordination strategy. On the other hand, den Otter et al. (2004) found a greater reduction in peak soleus EMG activity at slower walking speeds than in peak gastrocnemius EMG activity, so fiber composition may not always be a strong predictor of muscle function. Finally, our analysis did not include a calculation of contributions from centrifugal and Coriolis forces. While these forces can make significant contributions to joint angular accelerations during the swing phase of fast walking (Arnold et al., 2007), their

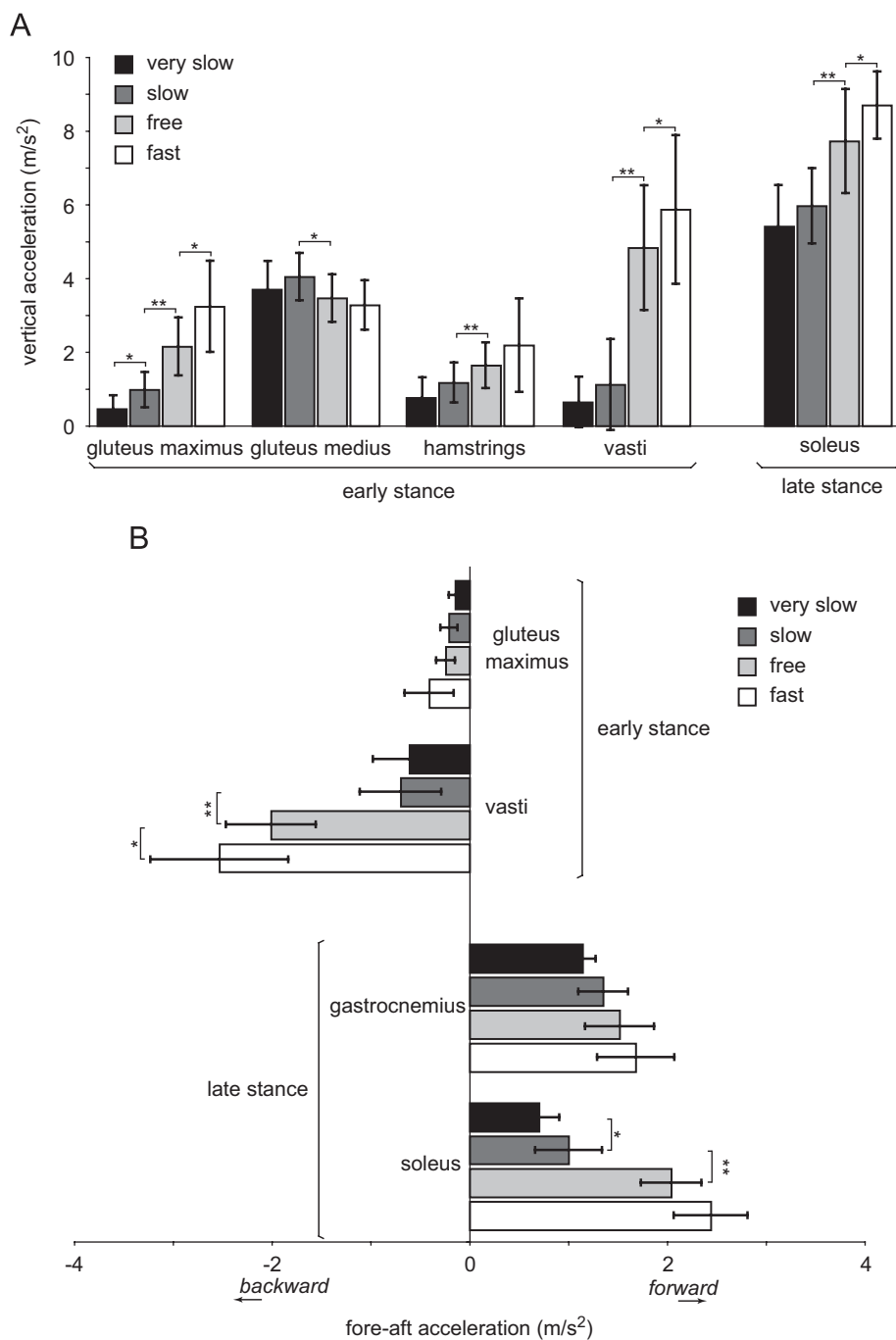


Fig. 6. Mean peak vertical (A) and fore-aft (B) accelerations of selected muscles from 8 subjects. Error bars span \pm one standard deviation. * $p < 0.05$ for within-subjects repeated contrasts analyses. ** $p < 0.01$ for within-subjects repeated contrasts analyses.

contributions to the linear accelerations of the mass center during walking are small (Anderson and Pandy, 2003).

In general, it is not possible to reproduce the results of simulation studies, because the software and models used to create and analyze the simulations are not available. This situation has created a barrier to the use of simulations in movement science. As a first step in overcoming this problem, this study has produced a collection of 32 subject-specific simulations of walking at various speeds that are available for analysis in a freely available software system so that others can reproduce our

results and perform additional analyses (Delp et al., 2007; <http://simtk.org>). These simulations, and the data on which they are based, provide reference data for a variety of future studies of normal and pathological gait.

Conflict of interest statement

None of the authors had any financial or personal conflict of interest with regard to this study.

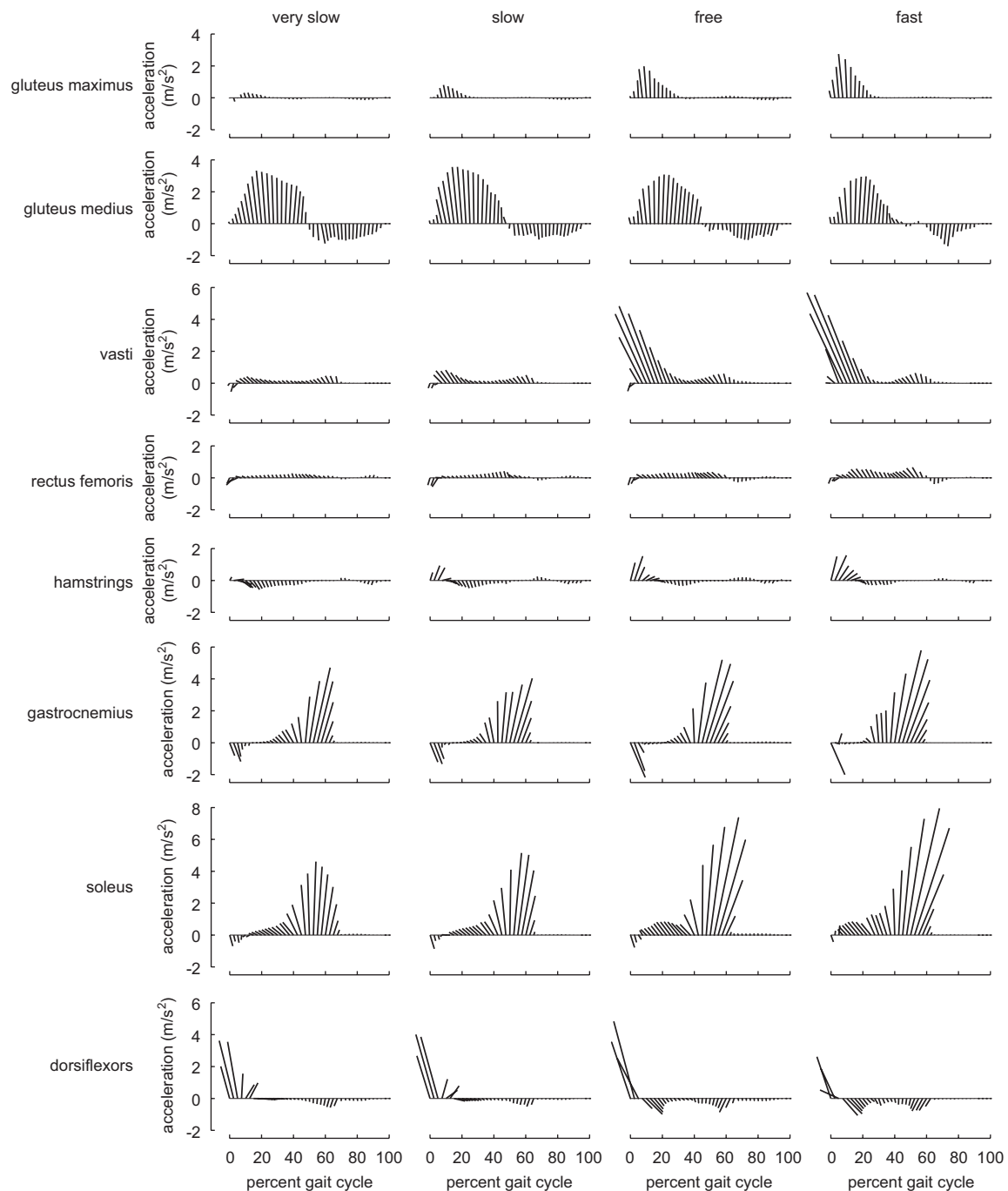


Fig. 7. Contributions to the acceleration of the body mass center from selected muscles across walking speeds. Each ray is the resultant vector of the vertical and fore-aft accelerations, averaged across eight subjects.

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